THE INTERRELATIONSHIPS OF THE SPECIES OF THE GENUS LYCAENA FABRICIUS (LEPIDOPTERA, LYCAENIDAE).

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Some years ago Dr. A. Glenn Richards, Jr., and the author began work together on a study of the male genitalia of the species of *Lycaena,* with the special purpose of finding our what these organs might show regarding the interrelationships of the species. Since then various changes of residence have prevented the completion of this study as a joint undertaking; the present writer has finally succeeded in bringing the task to a point of at least approximate completion.

Obviously to be of the greatest value, such a study could not be confined to the Nearctic species, although these constitute the major interest of the writer. Accordingly the majority of the species of the world have been included; it is believed that the small minority that were unobtainable are not of great phylogenetic significance.

The writer is greatly indebted to Dr. Richards, who contributed much of the material and made many of the dissections, to the American Museum of Natural History, to Cornell University and Mr. W. P. Comstock for the loan of specimens, to Dr. W. Schaus for his very kind gift of a specimen of the rare *L. pyrrhias* Godman & Salvin, and to Dr. J. McDunnough and Messrs. N. D. Riley and Foster H. Benjamin for aid in clearing up synonymic tangles. All of Dr. Richards' and the author's specimens have been deposited in the American Museum.

Structures of the Male Genitalia.

(see especially figs. 1, 2 & 8).

The genitalia of the species of *Lycaena* are of the conventional, rather specialized, Lycaenid type, differing strongly in the dorsal structures from most other butterflies. The homologies of these structures with the similarly located organs of the majority of other Lepidoptera are somewhat uncertain, and so the terms "labides" and "falces" have been used here. It is probable that the labides are developments of the tegumen, while the falces may represent modifications of the uncus; but careful comparative and embroyological studies should be made to determine these points.

The labides (*lab*), rounded, hairy lobes, are nearly always well developed, as are also the falces (*fal*), which are long, sharp,

heavily chitinized and strongly curved. The tegumen (*teg*) evidently constitutes the dorsal part of the genitalic "ring", while the extent of the vinculum is, in most cases, obvious. The caudal edges of the tegumen are folded in toward the mid-line beneath the anus, and are often more or less chitinized there, forming a subscaphium (*ssc*) which supports the anus.

This infolding continues cephalad and centrad as a membrane which envelops the oedeagus (*oed*), and is continuous with a similar fold that extends from the region of the bases of the harpés. In this latter fold there is considerable chitinization for the support of the oedeagus. For simplicity the term "juxta" (*jux*) has been used for the single, ventral, median portion of this oedeagus support, which lies between the sacculi of the harpés and fastens them together; and the term "anellus" (*an*) has been used for the expanded, paired, upper parts. These latter consist of two paired folds; the inner ones, which are the larger, form more or less of a trough for the support of the oedeagus; the outer ones consist of two arms which articulate with the upper, basal angles of the two harpés. Possible the latter may represent homologues of the transtilla in other Lepidoptera.

The oedeagus is more or less open dorsally, being thus for its terminal portion in the form of a trough; the ejaculatory duct (*ej. d.*) opens from it on the dorsal side, usually at about two-thirds from the base, and is provided with a single, triangular cornutus.

In the majority of the Nearctic species the saccus is very small; in many of the Palaearctic species it is of considerable length.

The harpé shows a great deal of modification, both in shape and in the development of chitinized ridges and teeth which are especially prominent in some of the Palaearctic species (*hippothoë, sarthus, virgaureae,* etc.). Occasionally it is greatly reduced in size, as in *li.* On the whole the developments of the harpé appear to be largely specific, and so cannot be used as safely in determining the relationships of the species groups as other less mutable characters.

Taxonomy.

It would be fallacious to expect a study such as the present one, based largely on a single set of organs, to furnish all the data necessary for the working of a complete phylogeny. The male genitalia appear to be almost invariably distinctive for each species, and to furnish excellent characters for species differentiation; but in many species they fail to give any reliable clue to relationship

with other members of the genus. In such cases the author has chosen to follow the path of discretion and refrain from arbitrary action based on guesswork, merely presenting the data for future consideration when material may be available for comparative studies of female genitalia and early stages.

In other cases, however, there occur such definite similarities of structure as to clearly indicate almost undoubted relationships. Systematic changes based on such cases have been made, even though they represent a considerable departure from the hitherto accepted classification. Previous ideas of the relationships of the Coppers have been based almost entirely on wing shape, color and pattern, characters which are notoriously changeable and therefore likely to be unreliable for phylogenetic purposes. While such characters have been by no means ignored in the present work, they have not been considered as important as definite similarities or differences in the genitalia. Thus, because of a very close resemblance of all its genitalic structures to those of a number of Palaearctic species, *cupreus* Edw. has been placed in the typically Palaearctic subgenus; and similarly *sarthus* Stgr., *caspius* Led. and *athamanthis* Ev. have been placed in the typically Nearctic subgenus.

Just what categories to use in formulating an intrageneric classification of *Lycaena* has been considerable of a problem. Certainly, because of insufficient dissimilarities and the presence of many annectant forms, not more than one genus would seem justified. Largely because of the presence in the Palaearctic of a number of single, isolated species, the exact relationships of which are at present indeterminable, the use of a number of subgenera alone was ruled out. Such a procedure would result in a disproportionate ratio of subgenera to species, and would necessitate the proposal of a considerable number of new names of doubtful worth.

It was finally decided to make use of but two subgenera, *L.* (*Lycaena*) for the series of typically Palaearctic species, and *L.* (*Tharsalea*) for the typically Nearctic series. In *L.* (*Lycaena*) must be included only one species of Nearctic distribution, *cupreus* Edw., and the sole Neotropical Copper, *pyrrhias* Godm. & Salv., besides the North American race *hypophlaeas* of the Palaearctic *phlaeas* L. Conversely only three species of Palaearctic occurrence are included in *L.* (*Tharsalea*).

In each subgenus the species have been divided into "species groups." In the Palaearctic series this seems a bit awkward

because of the presence of a number of isolated species, each of which, showing no definite resemblance to any other, must be placed in a species group by itself. But in view of the close similarity of structure between members of some of the larger species groups, nothing else could well be done; and the result is probably far more natural than would be the case if any of these isolated species had been "lumped" together.

The linear arrangement of the species groups is largely one of convenience only, and is not to be construed as representing throughout any theories of relationship and phylogeny. In some cases, such as the placing of *kasyapa* between the *thersamon* and *dispar* groups, the arrangement expresses a relationship, as is brought out in the discussion of the groups. But in much of the remainder of the Palaearctic series, and in the larger part of the Nearctic, interrelationships are so inconclusively shown by the genitalia that it seems the part of wisdom to do nothing definite in this respect.

Check-List of Species Studied.

Genus *Lycaena* Fabricius, type *Papilio phlaeas* L.
  Subgenus *Lycaena*
    thersamon group
      thersamon Esp.
      phoebus Blach.
      solskyii Ersch.
      thetis Klug
    kasyapa group
      kasyapa Moore
    dispar group
      (*dispar* L.)
        (a) *rutilus* Wernb.
      splendens Stgr.
      orus Cram.
      pavana Koll.
      standfussi Gr.-Grsch.
    phoenicurus group
      phoenicurus Led.
    pyrrhias group (*Iophanes* Draudt)
      pyrrhias Godm. & Salv.
    alciphron group
      alciphron Rott.
      cupreus Edw.
        (a) *snowi* Edw.

virgaureae group (*Heodes* Dalman)
virgaureae L.
dorilis Hufn.
phlaeas group (*Lycaena* Fabr. *sens. strict.*)
phlaeas L.
(a) *abbotti* Holland
(b) *Feildeni* McLach.
(c) *hypophlaeas* Bdv.
amphidamas group
amphidamas Esp.
li group
li Oberth.
pang Oberth.
boldenarum group
boldenarum White
salustius group
salustius Fabr.
enysii Butler
hippothoë group
hippothoë L.
Subgenus *Tharsalea* Scudder, type *Polyommatus arota* Bdv.
sarthus group
sarthus Stdgr.
caspius Led.
athamanthis group
(*athamanthis* Ev.)
(a) *alexandra* Püng.
arota group (*Tharsalea* Scud. *sens. strict.*)
arota Bdv.
(a) *virginiensis* Edw.
hermes group
hermes Edw.
xanthoides group (*Gaeides* Scud. & *Chalceria* Scud.)
xanthoides Bdv.
(a) *dione* Scud.
editha Mead
rubidus Behr
(a) *sirius* Edw.
gorgon group
gorgon Bdv.
heteronea Bdv.
(a) *gravenotata* Klots

thoë group
thoë Guér.
epixanthe group (*Epidemia* Scud.)
epixanthe Bdv. & Lec.
(a) *amicetus* Scud.
anthelle Dbldy *non pub.*
phaedrus Hall
dorcas Kirby
amicetus Dbldy. *non pub.*
anthelle Scud.
florus Edw.
(a) *helloides* Bdv.
nivalis Bdv.
mariposa Reak.

Discussions of Groups

thersamon group (fig. 1)

The most outstanding characteristics of this group are: the very long, pointed lobes of the anellus; the moderately long, heavy juxta; the short saccus; the harpé, broad at base, tapering to a moderately slender tip which is armed in some species with small, infolded teeth or rugosities.

In these characters the species agree well with one another, and form a compact group of evidently closely related forms. They are also well connected together in color and pattern. Structurally they are differentiated best by the shape of the harpé, which furnishes excellent characters.

kasyapa group

In *kasyapa* the lobes of the anellus are considerably shorter and broader, and the saccus is longer than in the *thersamon* group; in these characters it approaches the *dispar* group. The juxta is, however, very short, more so than in any of the *thersamon* species. This would preclude placing it in the *dispar* group with which, however, it evidently forms an annectant.

dispar group (fig. 2)

The most outstanding characteristics of this group are: the long, slender juxta; the moderately long saccus; the reduction in width of the tegumen, labides and falces. The harpé usually broadens somewhat at the tip, and is there armed with short, infolded teeth.

In these characters *dispar, splendens, pavana* and *orus* agree

well with each other, and are evidently closely interrelated. They differ from each other mainly in the shape of the harpé, which is longest and narrowest in *dispar,* and shortest and broadest in *orus*; in the shape of the oedeagus, which is very similar in *dispar, pavana* and *splendens,* but is comparatively little curved in *orus*; and in the length of the saccus, which is longest in *dispar* and shortest in *orus.* Distally the harpé of both *orus* and *standfussi* is somewhat more produced dorsally than ventrally, much as is shown in *pyrrhias* (fig. 3) and a number of other species. The juxta of *standfussi* is comparatively shorter than in the other three species. It seems as if *orus* represents a transitional form between *dispar* and *splendens* on the one hand and *standfussi* on the other, and then as if *standfussi* still further connects the group to the *thersamon group.* In this connection the fundamentally similar underside patterns of *orus* and *standfussi* are noteworthy.

phoenicurus group (fig. 4)

In its very short saccus and reduced anellus lobes, *phoenicurus* differs strongly from the *dispar* group; its juxta is also rather peculiar, being long but fused for a considerable distance with the sacculi of the harpés. In general its structures appear to show somewhat of a relationship to the *dispar* group, sufficient to warrant postulation of at least a slight degree of relationship.

pyrrhias group (fig. 3)

In *pyrrhias* the juxta is very short, which would seem to preclude a close relationship to the *dispar* and *thersamon* groups. The very long lobes of the anellus would seem, however, to place it somewhere in this vicinity, just as the slender, upcurved oedeagus also shows that it cannot be very closely related to any of the characteristic Nearctic species. In view of its peculiarities of structure, as well as of its peculiar position as the only Neotropical *Lycaena, pyrrhias* well deserves a position in a species group by itself. Its relationship is undoubtedly with the Palaearctic rather than with the Nearctic series, and is possibly rather ancient.

alciphron group (fig. 7)

The two members of this group, *alciphron* and *cupreus,* are very alike in genitalia; they differ essentially only in the length of the juxta, which is slightly longer and more curved in *alciphron,* and in the shape of the distal part of the harpé. Both agree with the *virgaureae* group in the possession of a spine near the dorsal margin of the harpé; but from this group they differ strongly in the

shape of the harpé, in the toothing of the distal part of the harpé, and in their longer saccus. Because of fundamental similarities in these three features they would seem to be more closely related to the *dispar* group, in spite of the dorsal spine on the harpé and the much smaller lobes of the anellus. As might be expected, *alciphron* is slightly more like the *dispar* group than is *cupreus*.

The two North American forms, *cupreus* and *snowi,* are so much alike in genitalic structure that I hesitate to recognize them as separate species. The harpé of *snowi* appears to average slightly shorter and broader than that of *cupreus*; the dorsal, subterminal tooth on the harpé of *cupreus* averages larger than that of *snowi*. Careful study of the early stages, of the distribution, and of large series of the two forms must be made. For the present I am treating *snowi* as a race of *cupreus,* which is all that the genitalic structures warrant.

virgaureae group (fig. 6)

In the two species placed here, *virgaureae* and *dorilis,* the genitalia are so very similar that there can be no doubt that a very close relationship exists between the two. The harpé is wide, strongly "spoon-shaped," and bears a strong, triangular, infolded flap near the tip and slightly above the ventral margin; a strong, heavily chitinized spine points inward from its dorsal margin. In both the saccus is very short, and the falces are considerably reduced in size, while the labides are not.

Virgaureae and *dorilis* differ structurally from each other mainly in the shape and size of the anellus lobes; in *dorilis* these are slightly longer and more pointed than in *virgaureae*.

The shape of the harpé, as well as other structures, is so distinctly different from the condition found in the *alciphron* group, that I believe that the dorsal spine, which occurs in both groups, cannot be taken as an evidence of relationship; it may well have been developed independently.

phlaeas group (fig. 5)

Phlaeas shows no very distinctive structural characters, and may be regarded as comparatively unspecialized. The harpé is rather wider and somewhat less heavily chitinized than in the majority of other Coppers, and bears an infolded, chitinized ridge near the tip; it is thus similar to that of *virgaureae,* but shows no trace of the dorsal spine characteristic of that species. Possibly there is a relationship.

In studying a considerable series of specimens no constant difference was found between the genitalia of *p. phlaeas, p. hypophlaeas,* and *p. abbotti.* Even color and pattern differences between the two are relatively slight; so that the placing of *hypophlaeas* as a race seems thoroughly justified. *Feildeni* is, of course, another race, from the far Arctic regions; Holland's placing of it as a separate species is an example of extreme "splitting."

amphidamas group (fig. 8)

Like *phlaeas, amphidamas* shows no outstandingly distinctive characteristics such as would aid in determining its relationships to other species of *Lycaena.* The small, sharply triangular lobes of the anellus are rather different from those of any other species; likewise peculiar is the development of a small but heavily chitinized subscaphium. Except for this latter structure it is not unlike the two species studied of the *li* group, being rather closer to *pang* than to *li.*

li group (fig. 9)

The two species here included, *li* and *pang,* show in addition to the very distinctive pattern of the under side of the secondaries, a characteristic reduction in the size of the harpé that sets them apart from the other species of *Lycaena.* The latter character is more noticeable in *li* than in *pang.* In *pang* the tegumen is proportionately much broader than in *li,* which may point out a connection to the following three species groups. The distal portion of the oedeagus of *pang* is considerably reduced in size.

Probably *tseng* Oberth. and *ouang* Oberth. also belong in this group.

boldenarum group (fig. 10)

The most characteristic feature of the genitalia of *boldenarum* is in the structure of the lobes of the anellus, which are long, broad, and rounded at their ends; the tegumen is very broad, and the distal portion of the oedeagus considerably reduced in size. In one specimen examined there appear to be three cornuti. On the basis of the genitalia, no definite relationship of *boldenarum* to other Coppers can be traced with any security. Its small size, peculiar coloring and pattern, and geographic distribution also set it apart.

salustius group

Genitalically the species of this group show no distinctive characteristic such as would aid in determining their relationships. In general they resemble the other comparatively unspecialized species

such as *phlaeas* and *amphidamas*. They are distinct from each other, differing in the shape of the harpé and the size and shape of the lobes of the anellus. Unquestionably they show no particular relationship to *boldenarum*. Possibly a careful study of their early stages will furnish a clue to their relationship.

hippothoë group (fig. 11)

Outstanding characteristics of *hippothoë* are: the very heavy oedeagus, the base of which is very strongly bent dorsad; the great specialization of the harpé, which has developed two distal processes each bearing a long, strong spine; the very peculiar shape of the juxta and anellus; the long saccus. Excepting the saccus, nothing resembling these occurs in any other species of *Lycaena* studied, save that there is a certain similarity in the harpé of the *sarthus* group. These distinctive specializations of the genitalia render futile any guesswork at the relationships of *hippothoë* based on these organs.

sarthus group (fig. 12)

With this group begins the subgenus composed of species, mostly Nearctic, in which the oedeagus is strongly bent ventrad. In all of these the saccus is short and weak, and the juxta and anellus, especially the former, somewhat reduced. Without doubt *sarthus* and *caspius* belong here, rather than with the other Palaearctic species in *L.* (*Lycaena*), as far as genitalic characters are concerned.

Sarthus and *caspius* are structurally very much alike, differing mainly only in the shape of the harpé which in *caspius* is a little more slender. The writer has only a few specimens for comparison, but is under a very strong impression that the two forms may be really members of a single species.

athamanthis group (fig. 26)

Athamanthis undoubtedly has close Nearctic relationships, as is evidenced by the structure of nearly all the parts of the male genitalia, but especially by the heavy, downcurved oedeagus and the shape and armature of the harpé. The position of the falces suggests a possible relationship to the *arota* group. The anellus lobes are rather like those of the *xanthoides* group, but are also similar to those of a number of Palaearctic species. The saccus is a trifle longer than that of any Nearctic species. These characters are rather indeterminate as regards exact relationships, so that beyond placing it here in the typically Nearctic subgenus nothing more can definitely be done for the present.

arota group (figs. 13, 14)

The chief characters which separate *arota* and *virginiensis* from the other species of *Lycaena* are the long, slender, unarmed harpé and the position of the falces, which are so strongly curved toward the meson that they practically lie in a transverse plane. In spite of their common possession of a tail at the anal angle of the secondary (a most untrustworthy character in *Lycaena*), *arota* and *virginiensis* show no close relationship at all to *hermes,* and Scudder's inclusion of all three in the genus *Tharsalea* would seem to have been unwarranted. There would be more justification for the separation of *arota* and *virginiensis* from all of the other Nearctic species of *Lycaena,* including *hermes,* using *Tharsalea* as a subgenus for them alone.

I have been unable to find any constant genitalic difference between *arota* and *virginiensis* (the specimens figured are extremes, but are connected by every degree of intergradation in other specimens), and I therefore strongly suspect that they are really members of a single species. *Virginiensis* may represent a color form which has become dominant east of the Sierras, forming a "race" there, though constituting only a color form in California. Such an explanation is perfectly in accord with genetical theory.

hermes group (fig. 15)

Structurally *hermes* is distinguished by the rather considerable development of the subscaphium (a character which likewise occurs in the *gorgon group*) and by the extreme reduction of the juxta. The lobes of the anellus, though lightly chitinized, and rounded, are of good size for a Nearctic species. The harpé is very similar in shape and armature to that of the following two species groups. Evidently *hermes* is, structurally at least, far closer to *gorgon* and *heteronea* than to its tailed Nearctic congeners.

xanthoides group (figs. 16–19)

The species here included are characterized by the structure of the anellus lobes, which are larger than in any others of the typically Nearctic series, and are pointed caudally; and by a somewhat less wide tegumen than is shown by most of the other Nearctic species. The juxta shows the double-curved condition also characteristic of the other related groups, but is considerably heavier than in any other Nearctic group. The falces are bent at nearly a right angle, a condition also found in the *gorgon* and *epixanthe* groups, and very different from the more gentle and gradual curve characteristic of the majority of the Palaearctic species.

The species are best separated from one another by the shape and armature of the harpé; in this respect *editha* appears to be closer to *xanthoides* than to *rubidus*.

No constant genitalic difference has been noticed between *r. rubidus* and *r. sirius,* forms which are unquestionable races of a single species.

Genitalically *xanthoides* and *dione* differ only in the teeth on the inner surface of the harpé, which appear to average slightly smaller in *xanthoides* than in *dione*; and in the juxta, which averages slightly thicker in *dione* than in *xanthoides*. These differences are extremely slight, and I suspect that study of a large series would show them to be of no value. Accordingly *dione* has been placed as a race of *xanthoides*.

gorgon group (figs. 20, 21)

The two species of this group are characterized by the small, rounded lobes of the anellus, the narrow, tapering harpé, and the rather wide tegumen. The caudal margins of the latter are folded toward the mid-line to form a rather strongly chitinized subscaphium for the support of the anus. Structurally the two species are distinguishable from each other by the shape and armature of the harpé, and by the rather narrower tegumen of *heteronea*. They are probably more closely related to the species of the *epixanthe* group than to any others.

thoë group (fig. 27)

The relationship of *thoë* to the other typically Nearctic species is evidently close, but its exact position is a matter of some doubt. The shape of the harpé is similar to that of *rubidus,* but the lobes of the anellus are rounded and not pointed as in the latter species. The falces are rather more gently curved than in the majority of Nearctic species. For the present it seems best to place it in a species group by itself.

epixanthe group (figs. 22–26)

The four species placed here are evidently closely interrelated. They are easily distinguishable from each other by the shape of the harpé, but great care must be exercised in using this character, for a very slight degree of distortion, or difference in the angle at which this structure is viewed, may cause it to appear of a very different shape.

There has been considerable confusion in the literature with regard to *dorcas* and *epixanthe,* a part of which can be cleared up

here. Boisduval apparently applied MSS. names to northern examples of both these species, but these were never published by him. These were *amicetus* for an *epixanthe* form (presumably) and *anthelle* for a *dorcas* form; the *chirotype* of the latter is in the U. S. National Museum, ex. Boisduval, Oberthür and Barnes collections, and is, according to Mr. Benjamin, a *dorcas*. Both of these Boisduval MSS. names were listed by Doubleday (List Lep. Brit. Mus., *2*: 55), but as *nomina nuda,* unaccompanied by any description or diagnosis; they were therefore not officially published by Doubleday, and his mere listing of them was insufficient to validate them. Perhaps this is as well, for he very evidently had reversed Boisduval's application of them. This is shown by the fact that three of the four specimens which he mentioned under the designation of "Polyommatus anthelle Boisduval MS." are still in the British Museum, and are certainly *epixanthe* according to Mr. N. D. Riley, who very kindly examined them for me. Presumably Doubleday's other series, which he designated as "amicetus" were *dorcas*; these specimens have been lost.

The first validation of these names, as pointed out by Barnes and Benjamin, was by Scudder (1876, Bull. Buffalo Soc. Nat. Hist. *3*: 128). Here Scudder agreed with Boisduval, since *anthelle* is placed as a synonym of *dorcas,* and *amicetus* as a synonym of *epixanthe*. It is very doubtful if the former is worth retaining as a race, but the latter certainly is. In that case *phaedrus* Hall, described from Nova Scotia and Newfoundland, must be placed as a synonym of *amicetus*. The type locality of *phaedrus* is, of course, that of the holotype—Nova Scotia—but *phaedrus* does not differ appreciably from Newfoundland examples. On what material Scudder based his allocation of these names will probably always remain in doubt. The writer searched the collection of the Museum of Comparative Zoology, where Scudder's collection reposes, but was unable to find any material more pertinent than one Labrador specimen of *dorcas* from the Scudder collection.

Between *dorcas* and *helloides* no constant genitalic difference could be found, although a considerable series of each was studied. They are accordingly placed as members of a single species. They cannot, however, be regarded as strictly geographic subspecies, for there is a large overlap of their ranges. However, as shown by McDunnough (Can. Ent. 1922, *44*: 136), the ecological ranges occupied by the two forms are quite constantly different, and it is probable that they have different food-plants. In this respect the writer's own observations in Colorado and Wyoming agree well with those cited by McDunnough for Alberta.

To the majority of workers such a difference in habitat and probable difference in food-plant, combined with a large overlap in geographic distribution, may seem to constitute a reason for considering the two forms as separate species without further ado. With this viewpoint the present writer cannot agree. He can see no reason for holding to the idea that two strains can diverge only under the influence of differing geographic environments, and when separated by a geographic barrier.

Probably in addition to *geographic subspecies* there can be formed *host subspecies,* as influenced by a combination of space-isolation, environmental and food factors, *food-plant subspecies, habitat subspecies,* and various others, as well as combinations of more than one type. In the divergence of two strains there must be at least two primary factors, viz., the origin of inheritable differences to cause the divergence, and the presence of some sort of a barrier to prevent subsequent mixing of the strains, and consequent relegation of them to the status of mere variant (Mendelian) forms. The new inheritable character may affect any part or parts of the anatomy, ecology or genetics of the organism; dependent on this expression, and its "survival value," is our classification of the diverging strain as one or another kind of "subspecies."

Considering the problem of species differentiation in this light, it is seen that *dorcas* and *helloides* may well be considered as members of a single species; separated from each other by some barrier (genetical?) of which at present we know nothing, they have diverged along ecological rather than along structural lines.

The essential question, of course, is one of where to draw the line between "species" and "subspecies"; for both are essentially the same, differing only in degree. This question must at present be answered for himself by every worker in every different group of organisms, and will probably be answered differently by most workers in the same group. Obviously one of the best criteria that can be applied within so small a category as a genus, a group of closely related organisms, is the degree of structural differentiation between what are admittedly closely related, but obviously distinct, species in that genus.

Applying this criterion in the present case we see that in the great majority of instances, forms which evidently are closely related yet distinct species, are invariably easily and constantly separable by genitalic characters. Examples of this in *Lycaena* are the differences between the four species of the *epixanthe* group, between *gorgon* and *heteronea,* between *xanthoides, editha* and *rubidus,* between the species of the *thersamon* group, etc. These would

all seem to point to the necessity of our considering that the presence of some degree of structural differentiation is a necessary criterion of the separation of "species" in this genus. The writer therefore feels that his "lumping" of *arota* and *virginiensis,* of *xanthoides* and *dione,* of *cupreus* and *snowi,* and of *dorcas* and *helloides* is justified.

Summary

Study of the male genitalia of *Lycaena* furnishes data as to the interrelationships of many, but not all, of the species, and points to the following general conclusions:

(1) All of the species should be included in a single genus.

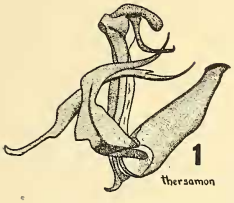
(2) The greater number of the Palaearctic species are more closely related to each other than to the majority of the Nearctic species, and *vice versa*; this is shown by similarities of structure and by the presence of annectant forms. For the Palaearctic series the nymotypical subgenus *L.* (*Lycaena*) is used; for the Nearctic series the subgenus *L.* (*Tharsalea*) Scudder. No further subgeneric divisions seem warranted at present.

(3) In the majority of cases, species that are distinctly separable from each other by well-marked color and pattern differences also show distinct and constant genitalic differences. It is therefore considered that the presence of genitalic differences may be established as a criterion of species separation in this genus.

Explanation of Figures.

All figures are based on tracings made with a camera lucida. No constant scale of enlargement was followed. The following abbreviations have been used:

an = anellus
ej.d. = ejaculatory duct
fal = falx
jux = juxta
lab = labis
oed = oedeagus
sac = saccus
scls = sacculus
ssc = subscaphium
teg = tegumen
vinc = vinculum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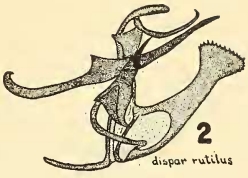
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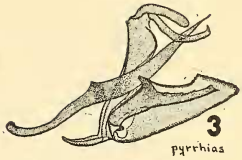
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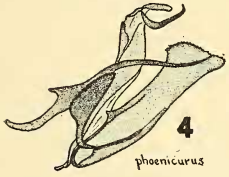
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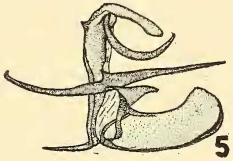
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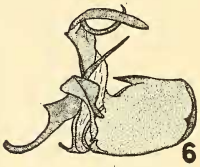
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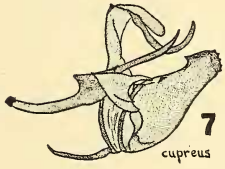
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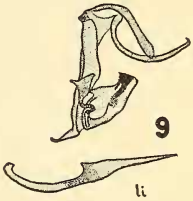
cupreus


8
amphidamas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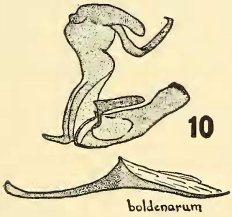
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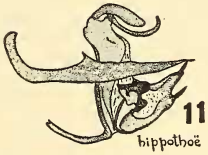
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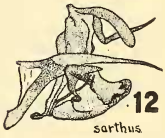
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sarthus


13
arota


14
virginiensis

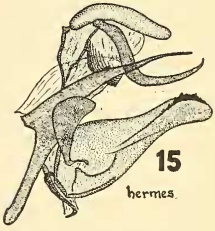
15
hermes

Plate VIII.

Fig. 1—*Lycaena* (*Lycaena*) *thersamon* Esp.
" 2— " " *dispar rutilus* Wernb.
" 3— " " *pyrrhias* Godm. & Salv.
" 4— " " *phoenicurus* Led.
" 5— " " *phlaeas* L.
" 6— " " *virgaureae* L.
" 7— " " *cupreus cupreus* Edw.
" 8— " " *amphidamas* Esp.
" 9— " " *li* Oberth.
" 10— " " *boldenarum* White
" 11— " " *thoë* L.
" 12— " (*Tharsalea*) *sarthus* Stgr.
" 13— " " *arota* Bdv.
" 14— " " *a. virginiensis* Edw.
" 15— " " *hermes* Edw.

Plate IX.

Fig. 16—*Lycaena* (*Tharsalea*) *r. rubidus* Behr.
" 17— " " *x. xanthoides* Bdv.
" 18— " " *x. dione* Scud.
" 19— " " *editha* Mead.
" 20— " " *gorgon* Bdv.
" 21— " " *h. heteronea* Bdv.
" 22— " " *e. epixanthe* Bdv. & Lec.
" 23— " " *nivalis* Bdv.
" 24— " " *mariposa* Reak.
" 25— " " *h. helloides* Bdv.
" 26— " " *athamanthis alexandra* Püng.
" 27— " " *thoë* Guer.